ON THE CHARACTERS OF THE SKULL IN THE HADROSAURIDÆ.

BY E. D. COPE.

In the year 1841, Professor Owen[1] distinguished the *Dinosauria* from other reptiles, as an order characterized by the structure of the sacrum, the limbs, and the articulations of the ribs with the vertebræ. The definition of the order remained without accession, until, in 1870, Prof. Huxley[2] determined the characters of the pelvis. This important addition to our knowledge placed the order on a firmer basis. No definitions were yet derived by either author from the skull, so that the relationships of the *Dinosauria* still remained obscure. In 1861 Professor Owen described part of the skull of a species of *Scelidosaurus* from the English Lias. On this imperfect basis I ventured in 1870[3] to determine whether the *Dinosauria* are monimostylicate or streptostylicate; and I added to the definition of the order, "attached quadrate;" and later[4] "os-quadratum articulated with its suspensorium by suture," thus placing these reptiles in the monimostylicate series. This character, if found to be general in the order, would distinguish it well from the *Lacertilia*, and give a point of affinity to the *Crocodilia*.

This order embraces a number of families. I at one time proposed to refer them to three suborders,[5] and Huxley concluded that they should be arranged in two suborders.[6] Professor Marsh, after showing that one of my three orders (*Symphypoda*) was established on characters erroneously ascribed to its type by previous writers, proposed to divide the *Dinosauria* into seven suborders. He later[7] regarded the *Dinosauria* as a subclass, and divided it into five orders, the fourth of which is composed of three suborders. The characters used by Marsh to define this supposed subclass, do not differ from those previously developed as above cited, excepting that a number are introduced which

[1] British Fossil Reptiles.

[2] Quarterly Journal of the Geological Society, p. 33.

[3] American Naturalist, 1871, p. 508.

[4] Proceedings Amer. Assoc. Adv. Science, 1870 (1871), p. 233.

[5] Transactions American Philosophical Society, xiv, 1869, 90-99.

[6] Quarterly Jour. Geolog. Soc., London, 1870.

[7] Amer. Jour. Sci. Arts, 1882, p. 83.

cannot be used to distinguish a subclass, or in some instances an order. In like manner, the definitions of his orders and suborders embrace many characters which are not usually regarded as defining groups higher than families. Such, *e. g.*, are the numbers of toes; relative sizes of fore- and hind-limbs; solidity or non-solidity of bones; presence or absence of dermal armor. Much light was, however, thrown on the subject by Professor Marsh, by the numerous characters he brought to light, and the number of forms he defined.

The constitution of the pelvis is shown by Marsh to differ materially in the different members of the *Dinosauria*. As this region presents characters diagnostic of the order *Dinosauria* itself, its modifications within the order become of importance. The ungulate or unguiculate character of the feet must also not be neglected, although of less importance than in the mammalia. If the order is susceptible of division into suborders, it must be by means of the following definitions, which I select from Marsh's diagnoses:

Feet ungulate; pubes projecting and connected in front; no postpubes; *Opisthocœla.*

Feet ungulate; pubes projecting free in front; postpubes present; *Orthopoda.*

Feet unguiculate; pubes projecting downwards and coössified distally; calcaneum not produced; *Goniopoda.*

Feet unguiculate; calcaneum much produced backwards; ? pelvis; *Hallopoda.*

I have used for these orders the oldest names when the definitions first given were not erroneous, although they were inadequate. Thus I think the name *Opisthocœla* (Owen[1]) must take precedence of *Sauropoda* Marsh. I combine Marsh's two divisions, *Stegosauria* and *Ornithopoda*, into one, and use the name I gave in 1866 and redefined in 1869,[2] for the division thus remodeled. The name *Goniopoda*, given at the same time, I designed to embrace the carnivorous *Dinosauria*, but included in my definition some characters which are of less significance than I then attached to them.

Prof. Huxley recognized three families; the *Scelidosauridæ* and

[1] Palæontology, 1860, p. 272.

[2] Transactions American Philos. Soc., xiv, p. 90. See American Naturalist, 1882, March.

Iguanodontidæ, which belong to the *Orthopoda*, and the *Megalosauridæ*, which pertains to the *Goniopoda*. To the former, I added the family *Hadrosauridæ* in 1869, and in 1877 I defined the *Camarasauridæ*, of the suborder *Opisthocœla*.[1] To this family Marsh gave, in 1882, the name of *Atlantosauridæ*.[2] At the same time he proposed a number of families, some of which will be retained, while others are not sufficiently defined.

The *Hadrosauridæ* are, so far as known, confined to the upper cretaceous beds of North America, and continued, with their accompanying carnivorous genera, later in geological time than any other *Dinosauria*. Besides the genus *Hadrosaurus*, I have added the genera *Diclonius* and *Cionodon*, and it is possible that the genera *Monoclonius*, *Dysganus* and *Agathaumas* also belong to it. These types are all found in the Laramie formation, excepting *Hadrosaurus*, which is as yet only known from the older Fox Hills or Mæstrichtian, and Pierre epochs. From the latter formations, came also *Hypsibema*, possibly a member of the same family.

As the latest in time, the *Dinosauria* of the Laramie possess an especial interest. Having recently obtained a specimen of a species of the genus *Diclonius* Cope, I am in a position to give not only the characters of the family and suborder more definitely than heretofore, but also to furnish some cranial characters of the order, which have been hitherto little known or unknown. The species on which these observations are made is the *Diclonius mirabilis*,[3] of Leidy. It is represented by a nearly complete skeleton, including the skull, which was discovered by Messrs. Wortman and Hill in the Laramie beds of Dakota. At present, I only describe the general characters, and those chiefly cranial, leaving the complete description and iconography for my forthcoming volume on the Laramie vertebrate fauna.

The character which distinguishes this genus from *Hadrosaurus* is the attenuation of the astragalocalcaneum, and its coössification with the tibia. *Ornithotarsus* differs from *Diclonius* in the pro-

[1] Proceedings American Philosophical Soc., 1877, p. 243.

[2] Amer. Jour. Sci. Arts, 1882, p. 83.

[3] This species is part of the one called by Leidy *Trachodon mirabilis*, who included in it a species of *Dysganus*. He did not characterize the genus *Trachodon*, and afterwards abandoned it. (Proceedings Academy, Phila., 1868, p. 199.)

duced calcaneum, which supports the extremity of the fibula. There are four digits of the anterior foot, and three of the posterior. The fore-limb is much shorter than the hind-limb, so that the attitude of the animal was kangaroo-like, as in *Hadrosaurus* and *Lælaps*. In this it differed from *Monoclonius*,[1] where the anterior limbs are as long as the posterior.

Ordinal Characters.—The quadrate bone is immovably articulated to the skull by three elements; the parietal, the quadratojugal, and the jugal. The intercalare occupies a position on the external edge of the exoccipital, and nearly approaches the proximal end of the quadrate at its posterior side. The postfrontals and prefontals are well developed, and the parietals, frontals, nasals and premaxillaries form the middle line of the skull above, as in other reptiles. The elements of the lower jaw belonging to reptiles are all present.

Subordinal and Family Characters.—The *parietal* is, as to its superior face, a T-shaped bone, of which the transverse portion rests on the supraoccipital bone, without interspace. The external extremities of the transverse branches are excavated below to receive the proximal end of the quadrate. These extensions of the parietal are stout, and represent the parietosquamosal arch of the *Lacertilia*. Resting as they do on the occipital, they present a character exactly intermediate between those presented by the *Crocodilia* and *Lacertilia*.

The *zygomatic arch* is complete, having the usual flexure observed in reptiles, and branching to a postorbital arch by the intervention of a postorbital bone. The postorbital part of the zygomatic arch forms the external border of the superior aspect of the skull, and encloses a crotaphite foramen. The portions of the frontal and parietal bones which separate the crotaphite foramina, form a narrow isthmus. The postorbital part of the zygoma consists chiefly of the squamosal. This element is rod-like, and does not reach or take part in the articulation with the quadrate. In this respect this genus differs materially from *Scelidosaurus*, where, according to Owen, the squamosal is more extended posteriorly, and articulates with the superior part of the quadrate by a fixed articulation. The external portions of the parietal are thus, in *Scelidosaurus*, correspondingly reduced.

The *malar* or *jugal* bone is of large size, while the quadrato-

[1] Proceedings Phila. Academy, 1876, October.

jugal is rather small. Its articulation with the quadrate is squamosal. The maxillary is convex on its outer face, presenting the teeth inwards. The nasals are distinct, and much narrowed forwards to their junction with the spines of the premaxillaries. The latter bones are distinct. They form, when viewed from above, an anchor-shaped body, with the curved flanges extending outwards and backwards. These enclose, with the anterior apex of the maxillaries, the huge external nareal orifices, which were probably roofed over by membrane, as in the birds.

The *pterygoids* extend well posteriorly as broad plates, and are in close contact with the inferior part of the quadrates. They are separated for a short distance on the middle line posteriorly by a fissure, which, with the narrow space between the pterygoids and the presphenoids, gives exit to the transversely narrowed posterior nares. The occipital condyle looks downwards. The sphenoid is posteriorly horizontal, and overlaps the basioccipital with only a trace of lateral tuberosities; but in front it is curved abruptly downwards. At this point, an elongate, flattened, truncate process extends posteriorly, forming the median part of the roof of the fissure of the posterior nares. In front of this fissure the pterygoids are in contact, and extend a considerable distance anteriorly; at least to opposite to the border of the large anterior palatomaxillary foramen.

The *maxillary* bone is produced far posteriorly, so as to define the zygomatic foramen on the inner side. The palatine bone extends posteriorly between it and the pterygoid for a considerable distance, when the expanding pterygoid cuts it off, and extends to the posterior extremity of the maxillary, closing the space occupied in the *Lacertilia* by the posterior palatomaxillary foramen. I cannot distinguish whether the portion which extends to the maxillary bone is distinguished as an ectopterygoid. The posterior edge of this part of the pterygoid projects below the posterior part of the bone, which is nearly horizontal until it reaches the quadrate. It then ascends, forming a lamina on the inner side of that bone, reaching the process from the inner side of the condyle.

The *vomer* is a narrowed, horizontal lamina between the anterior parts of the maxillary bones, anterior to which point it does not appear to extend. It soon becomes a vertical lamina, spreading at the base, where it is in contact with the middle line of contact of the pterygoid bones (and perhaps of the palatines, but these

are not visible at that point). From this point it is a deep attenuated keel, dividing the palate into two deep channels, and extends as far posteriorly as the nares. The posterior part is free beyond its base. The entire vomer is like that seen in various natatorial birds. The anterior maxillopalatine foramen separates the vomer from the maxillaries anteriorly. Posteriorly, the foramen is bounded by an ascending process of the maxillary bone, which is in contact with the palatines posteriorly.

The *premaxillary* is divided its whole length. At the middle line above, it passes between the nasal laminæ, while below it forms the roof of the muzzle part of the mouth, and the floor of the huge nareal fossa on each side of its spine. This part extends posteriorly as a thin lamina, each meeting that of the opposite side on the middle line, and recurving upwards, forming a median superior crest. The horizontal portion extends above the maxillary bone, between it and the descending postnareal part of the nasal, and extends over the anterior part of the lachrymal, intervening between the anterior extremity of the malar, and the posterior extremity of the nasal. Its posterior portion develops a rib-like projection, which descends downwards and forwards towards the anterior part of the maxillary bone, and disappears. This bone perhaps includes the *maxilloturbinal*.

The preorbital region includes a not unusual arrangement of the elements. The prefrontal bone descends as far as the middle of the anterior border of the orbit, and to the lachrymal. The orbital edge of the latter is interrupted by an element which presents a vertical edge outwards, and appears to be distinct from it, extending under it anteriorly, and separated from it by a vertical groove externally. It is, perhaps, the superciliary bone of Cuvier, which occupies a somewhat similar position in the *Varanidæ*. Below the lachrymal a small part of the orbit is bounded in front by the jugal. The latter sends forward a laminar prolongation over the maxillary, separating it externally from the posterior extension of the maxilloturbinal.

The *mandibular ramus* includes all the elements of the reptilian jaw. The arrangement posteriorly is a mixture of that of the crocodile and that of the lizard, while the remaining portion is peculiar. The angle is formed by about equal parts of the articular and angular, the former furnishing the external half, the latter the internal. There are a huge dental fossa and foramen, as in the

Lacertilia, and no perforations either external or internal, in agreement with the same type. The coronoid process is very large and elevated, and its base, which is crescentic in section, is embraced by the surangular, and is reached posteriorly by the anterior prolongation of the articular. Its posterior face is concave, and its apex is curved anteriorly, reaching the superior edge of the jugal bone at the inferior border of the orbit. The angular bone forms the internal border of the dental fossa, and extends to the posterior edge of the splenial above. Below, it sends a prolongation forwards. The greater part of the external and inferior faces of the ramus are formed by the surangular bone, which has an enormous extent, far exceeding in size that of any known reptile. It extends posteriorly to below the quadrate cotylus. Anteriorly it spreads laterally, and unites with its fellow of the opposite side, forming a short symphysis, and simulating a dentary. At the base of the internal side of the ramus, it is separated from the anterior prolongation of the angular by an open Meckelian groove, which shallows out near the middle of its length. In correspondence with this extent of the surangular, the splenial is enormously developed, and contains the great magazine of teeth which I have described as characteristic of this type.[1] Its internal wall is very thin, and adheres closely to the faces of the teeth, in the fossil, in its present condition. This development and dentition of the splenial bone distinguishes the *Hadrosauridæ* widely from the *Iguanodontidæ*. The dentary bone is a flat semicircular plate attached by suture to the extremities of the surangulars. There is no trace of symphysial suture, and the posterior border sends a median prolongation backwards, which is embraced by the surangulars. The edge of the dentary is flat, thin, and edentulous, and closes within the edge of the premaxillary.

The dentition is remarkable for its complexity, and for the difference in character presented by the superior and inferior series. Leidy pointed out the character of the latter[2] in the *Hadrosaurus foulkei*, and I have described the character of the superior dentition in the genera *Cionodon*[3] and *Diclonius*.[4] The teeth of both

[1] Bulletin U. S. Geol. Survey Territories, F. V. Hayden; iii, p. 594–7. May, 1877.

[2] Cretaceous Reptiles North America, 1864, p. 83.

[3] Vertebrata of Cretaceous formations of the West, 1875, p. 59.

[4] Proceedings Philadelphia Academy, 1876, p. 250.

series succeed each other in columns of from five to eight teeth each, following an arc of a circle. The superior arc is convex externally; the inferior arc is convex internally, or towards the position of the tongue. It results that the opposed grinding surfaces of the two dental series are vertical. The cementum-plate of the tooth is, in both sets, on the convex side of the tooth, hence external and inferior in the superior teeth, and internal and superior in the inferior teeth. The teeth replace each other differently in the two jaws, or rather the replacement of the teeth does not partake of the general reversal of relations which the opposite series present in all other respects. The successional teeth rise in both jaws on the inner sides of the older teeth. From this it follows, that in the superior series the replacement is on the non-functional side of the tooth, or from the side which does not bear the cementum-plate. In the lower jaw, the successional teeth follow on the side that bears the cementum-plate, so that one tooth must be worn away before the apex of its successor can come into use. The arrangement of the superior series permits the successional to overlap the functional tooth far beyond the base of the enamel-plate, which in point of fact they do in the *Diclonius mirabilis*, though not to the same extent as in the *Cionodon arctatus*. The superior teeth are smaller and narrower in form than the inferior, and both have a keel on the median line of their cementum-face. There are no teeth on the anterior parts of the surangular bone nor on the dentary or premaxillary bones. The extremity of the muzzle is a flattened spatulate beak.

Dermal or corneous structures have left distinct traces in the soft matrix about the end of the beak-like muzzle. Laminæ of brown remnants of organic structures were exposed in removing the matrix. One of these extends as a broad vertical band round the sides, indicating a vertical rim to the lower jaw, like that which surrounds some tea trays, and which probably represents the tomia of the horny sheath of a bird's beak. At the front of the muzzle its face is sharply undulate, presenting the appearance of vertical columns with tooth-like apices. Corresponding tooth-like processes, of much smaller size, alternate with them from the upper jaw. These probably are the remains of a serration of the extremital part of the horny tomia, such as exist on the lateral portions in the lamellirostral birds.

Systematic Results.—The structure of the skull of this species adds some confirmation to the hypothesis of the avian affinities

of the *Dinosauria*, which I first announced, as indicated by the hind-limbs, and which Professor Huxley soon after observed in the characters of the limbs and pelvis. The confirmation is, however, empirical rather than essential, and is confined to a few points. One of these is the form and position of the vomer, which much resembles that seen in lamellirostral birds. The large development of the premaxillary bone has a similar significance. So has the toothless character of that bone and the dentary.

Among reptiles, this skull combines, in an interesting way, the characters of the two orders *Crocodilia* and *Lacertilia*. The presence of the ethmoid above the maxillary and overlapping the lachrymal, is unique among vertebrata, so far as I am aware. The free exoccipito-intercalare hook is scarcely less remarkable.

Of mammalian affinity there is no trace to be found.

Specific Characters.—The general form and appearance of the skull, as seen in profile, is a good deal like that of a goose. From above it has more the form of a rather short-billed spoonbill (*Platalea*). For a reptile, the head is unusually elevated posteriorly, and remarkably contracted at the anterior part of the maxillaries. The flat, transverse expansion of the premaxillaries is absolutely unique. The posterior edges of the occipital bones are produced far backwards, forming a thin roof over the anterior part of the vertebral column. This roof is supported by two strong buttresses, one from each side of the foramen magnum. The latter is a vertical oval. The exoccipital (carrying the intercalare) descends on each side, forming a free hook-like process behind the superior half of the quadrate. The recurved process of the lateral branches of the parietal underruns the squamosal two-thirds the length of the latter. The quadrate is separated by a rather narrow, obliquely vertical fossa, from the postorbital arch, owing to the posterior position of the latter.

The orbit is posterior in position, and is a horizontal oblong in form. The superior (superciliary) border is flat, with slight rugosities at the positions of the pre- and postfrontal sutures. The frontal region is a little concave, and there is a convexity of the superior face of the prefrontal bone in front of the line of the orbit. The peculiar position of the teeth gives the side of the face, when the mandible is closed, a horizontally extended concavity. There are four and a half tooth-like colums on each side of the middle line of the end of the muzzle.

The extremital teeth of both series are smaller than the great majority, which are of equal size and similar form. Those of the superior series are rod-like, narrowed at the extremities, and flattened on one side. The edges of the cementum-plate are not serrate, and the other faces of the tooth are finely rugose with cementum-granules. In the inferior series, the cementum-faces are diamond-shaped, and the tooth may thus be distinguished into crown and root. The concealed surfaces are finely rugose; the edges of the cementum-plate are not serrate, and its surface is smooth. As compared with the *Hadrosaurus foulkei*, the dental magazine is much deeper, and contains a greater number of teeth in a vertical column, and probably a larger number in the aggregate. I find in each maxillary bone of the *Diclonius mirabilis* six hundred and thirty teeth, and in each splenial bone four hundred and six teeth. The total number is then two thousand and seventy-two.

According to Mr. Wortman, who, with Mr. Hill, dug the skeleton out, its total length is thirty-eight feet. The length of the skull is 1·180 meters.

Restoration.—This animal in life presented the kangaroo-like proportions ascribed by Leidy to the *Hadrosaurus foulkei.* The anterior limbs are small, and were doubtless used occasionally for support, and rarely for prehension. This is to be supposed from the fact that the ungual phalanges of the manus are hoof-like, and not claw-like, though less ungulate in their character than those of the posterior foot. The inferior presentation of the occipital condyle shows that the head was borne on the summit of a vertical neck, and at right-angles to it, in the manner of a bird. The head would be poised at right-angles to the neck when the animal rested on the anterior feet, by the aid of a U-like flexure of the cervical vertebræ. The general appearance of the head must have been much like that of a bird.

The nature of the beak and the dentition indicate, for this strange animal, a diet of soft vegetable matter. It could not have eaten the branches of trees, since any pressure sufficient for their comminution would have probably broken the slightly attached teeth of the lower jaw from their places, and have scattered them on the floor of the mouth. It is difficult to understand also how such a weak spatulate beak, could have collected or have broken off boughs of trees. By the aid of its dentate horny edge

it may have scraped leaves from the ends of branches, but the appearances indicate softer and less tenacious food. Could we suppose that the waters of the great Laramie lakes had supplied abundant aquatic plants without woody tissue, we would have the condition appropriate to this curious structure. Nymphæas, Nuphars, Potamogetons, *Anacharis*, *Myriophyllum* and similar growths could have been easily gathered by this double-spoon-like bill, and have been tossed, by bird-like jerks of the head and neck, back to the mill of small and delicate teeth. In order to submit the food to the action of these vertical shears, the jaws must have been opened widely enough to permit their edges to clear each other, and a good deal of wide gaping must, therefore, have accompanied the act of mastication. This would be easy, as the mouth opens, as in reptiles and birds generally, to a point behind the line of the position of the eye. The eye was evidently of large size. On the other hand the indications are that the external ear was of very small size. There is a large tract that might have been devoted to the sense of smell, but whether it was so or not is not easily ascertained.

We can suppose that the huge hind-legs of this genus and of *Hadrosaurus* were especially useful in wading in the water that produced their food. When the bottom was not too soft, they could wade to a depth of ten or more feet, and, if necessary, drag aquatic plants from their hold below. Fishes might have been available as food when not too large, and not covered with bony scales. Most of the fishes of the Laramie period, are, however, of the latter kind (genus *Clastes*). The occurrence of several beds of lignite in the formation shows that vegetation was abundant.

EXPLANATION OF PLATES.

(All the figures are one-seventh of the natural size.)

PLATE IV. Side view of skull of *Diclonius mirabilis*.

PLATE V. The same viewed from above.

PLATE VI. Inferior view of the same.

PLATE VII. Fig. 1, View of occipital region of the same. Fig. 2, View of the extremity of the muzzle from the front.

The complete iconography of this species will appear in the third volume of the Report of the United States Geological Survey of the Territories, under F. V. Hayden and J. W. Powell, now in course of preparation.